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Adapting wheat in Europe for climate change

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Review

Adapting wheat in Europe for climate change[☆]M.A. Semenov^a, P. Stratonovitch^a, F. Alghabari^b, M.J. Gooding^{b,*}^a Computational and Systems Biology Department, Rothamsted Research, Harpenden, Herts AL5 2JQ, UK^b School of Agriculture, Policy and Development, University of Reading, Earley Gate, P.O. Box 237, Reading RG6 6AR, UK

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ABSTRACT

Increasing cereal yield is needed to meet the projected increased demand for world food supply of about 70% by 2050. Sirius, a process-based model for wheat, was used to estimate yield potential for wheat ideotypes optimized for future climatic projections for ten wheat growing areas of Europe. It was predicted that the detrimental effect of drought stress on yield would be decreased due to enhanced tailoring of phenology to future weather patterns, and due to genetic improvements in the response of photosynthesis and green leaf duration to water shortage. Yield advances could be made through extending maturation and thereby improve resource capture and partitioning. However the model predicted an increase in frequency of heat stress at meiosis and anthesis. Controlled environment experiments quantify the effects of heat and drought at booting and flowering on grain numbers and potential grain size. A current adaptation of wheat to areas of Europe with hotter and drier summers is a quicker maturation which helps to escape from excessive stress, but results in lower yields. To increase yield potential and to respond to climate change, increased tolerance to heat and drought stress should remain priorities for the genetic improvement of wheat.

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1. Introduction

Food security has become a major challenge given the projected need to increase world food supply by about 70% by 2050 (Anon., 2009). Considering the limitations on expanding crop-growing areas, a significant increase in crop productivity will be required to achieve this target (Parry et al., 2011; Reynolds et al., 2011). Wheat production is highly sensitive to climatic and environmental variations (Porter and Semenov, 2005). Global warming is characterised by shifts in weather patterns and increase in frequency and magnitude of extreme events (Lobell et al., 2012; Semenov and Shewry, 2011; Sillmann and Roeckner, 2008). Increasing temperature and incidence of drought associated with global warming are posing serious threats to food security (Lobell et al., 2013). Climate change, therefore, represents a considerable challenge in achieving the 70%-increase target in world food production. New wheat

cultivars better adapted for future climatic conditions will therefore be required. However, the intrinsic uncertainty of climate change predictions poses a challenge to plant breeders and crop scientists who have limited time and resources and must select the most appropriate traits for improvement (Foulkes et al., 2011; Semenov and Halford, 2009; Zheng et al., 2012). Modelling provides a rational framework to design and test *in silico* new wheat ideotypes optimised for target environments and future climatic conditions (Hammer et al., 2006, 2010; Semenov and Halford, 2009; Semenov and Shewry, 2011; Sylvester-Bradley et al., 2012; Tardieu and Tuberosa, 2010; Zheng et al., 2012). Eco-physiological process-based crop models are commonly used in basic and applied research in the plant sciences and in natural resource management (Hammer et al., 2002; Passioura, 1996; Rötter et al., 2011; Sinclair and Seligman, 1996; White et al., 2011). They provide the best-available framework for integrating our understanding of complex plant processes and their responses to climate and environment. Such models are playing an increasing role in guiding the direction of fundamental research by providing quantitative predictions and highlighting gaps in our knowledge (Hammer et al., 2006; Hammer et al., 2010; Semenov and Halford, 2009; Semenov and Shewry, 2011; Tardieu, 2003).

The objective of our study was to assess wheat yield potential under climate change in Europe and identify challenges which must be overcome to achieve high wheat yields in the future. Firstly, we used the Sirius wheat model to optimise wheat

Abbreviations: A, maximum area of flag leaf area; ABA, abscisic acid; CV, coefficient of variation; FC, field capacity; Gf, grain filling duration; GMT, Greenwich mean time; GS, growth stage; HSP, heat shock protein; LAI, leaf area index; HI, harvest index; Ph, phyllochron; Pp, photoperiod response; Ru, root water uptake; S, duration of leaf senescence; SF, drought stress factor.

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ideotypes for future climate scenarios (Jamieson and Semenov, 2000; Lawless et al., 2005; Semenov, 2009; Semenov and Stratonovitch, 2013). A wheat ideotype was defined as a set of Sirius cultivar parameters. By changing cultivar parameters, we change wheat growth and development in response to climatic and environment variations and can select ideotypes with better performance under future climates and environments. Sirius is a well validated model and was able to simulate accurately wheat growth and grain yield in a wide range of environments, including Europe, USA, New Zealand and Australia, and for experiments reproducing conditions of climate change, e.g. Free-Air Carbon dioxide Enrichment (FACE) experiments (Ewert et al., 2002; He et al., 2012; Jamieson et al., 2000; Lawless et al., 2008; Martre et al., 2006; Asseng et al., 2013).

Despite the current utility of Sirius, it remains a challenge for such models to capture the yield response of wheat to extreme events, particularly when they coincide with sensitive growth stages (Craufurd et al., 2013). Crop models need an overhaul to incorporate such responses to extreme weather events (Rötter et al., 2011). For example, it has been established that wheat yield is particularly sensitive to abiotic stresses during microsporogenesis, anther dehiscence and fertilization because of effects on grain set (as reviewed by Barnabas et al., 2008; Craufurd et al., 2013); and just after fertilization because of effects on grain size (Gooding et al., 2003). To facilitate model development additional data from carefully designed experiments will be required. The second approach presented here is, therefore, to describe the response of wheat to heat and drought stress as imposed at booting and anthesis, using pot-grown plants and controlled environment facilities.

2. Assessing yield potential of future wheat ideotypes

We selected ten sites for our study representing wheat growing regions in Europe (Table 1). Wheat ideotypes were described by nine model parameters used in the Sirius wheat model to describe wheat cultivars and considered as most promising for improvement of yield potential under climate change (Table 2). We used an evolutionary algorithm to optimize ideotypes for future climatic conditions as predicted by the HadCM3 global climate model.

2.1. Cultivar parameter space for optimisation

The ranges of parameter values used in optimization are presented in Table 2. The ranges were based on parameters calibrated by Sirius for modern cultivars allowing for variations reported in the literature for existing wheat germplasm (He et al., 2012; Semenov et al., 2009).

2.1.1. Photosynthesis

We assume that a 10% increase in light conversion efficiency could be achieved in the future. Using a model of canopy

photosynthesis, (Tambussi et al., 2007) showed that the value of parameter λ (Rubisco specificity factor that represents the discrimination between CO₂ and O₂) found in current C3 crops exceeds the level that would be optimal for the present CO₂ concentration ([CO₂]), but would be optimal for [CO₂] of about 220 ppm, the average over the last 400,000 years. The simulation results showed that up to 10% more carbon could be assimilated, if λ was optimal for the current [CO₂] level.

In Sirius, radiation use efficiency (RUE) is proportional to [CO₂] with an increase of 30% for doubling in [CO₂] compared with the baseline of 338 ppm, which is in agreement with the recent meta-analysis of field-scale experiments on the effects of [CO₂] on crops (Vanuytrecht et al., 2012). A similar response was used by other wheat simulation models, e.g. CERES (Jamieson et al., 2000) and EPIC (Tubiello et al., 2000).

2.1.2. Phenology

Three cultivar parameters are directly related to phenological development of wheat, i.e. phyllochron **Ph**, daylength response **Pp** and duration of grain filling **Gf** (Table 2). Modifying the duration and timing of crop growth cycle in relation to seasonal variations of solar radiation and water availability may have significant effects on yield (Akkaya et al., 2006; Richards, 2006). An optimal flowering time has been the single most important factor to maximise yield in dry environments (Richards, 1991). The phyllochron **Ph** is the thermal time required for the appearance of successive leaves, and is a major driver of phenological development (Jamieson et al., 1995, 2007, 1998a). Details of the response of final leaf number to daylength **Pp** could be found in Brookings et al. (1995); Jamieson et al. (1998b). By modifying phyllochron **Ph** and daylength response **Pp** we alter the rate of crop development and, therefore, the date of flowering and maturity. Increasing the duration of the grain filling period **Gf** has been suggested as a possible trait for increasing grain yield in wheat (Evans and Fischer, 1999). In Sirius, **Gf** is defined as a cultivar-specific amount of thermal time which needs to be accumulated to complete grain filling (Jamieson et al., 1998b). During grain filling, assimilates for the grain are available from two sources: new biomass produced from intercepted radiation and water-soluble carbohydrates stored mostly in the stem before anthesis. In Sirius, the labile carbohydrate pool is calculated as a fixed 25% of biomass at anthesis, and is translocated to the grain during grain filling. Increasing **Gf** will increase the amount of radiation intercepted by the crop and, consequently, grain yield. However, in the model, water-soluble carbohydrates accumulated before anthesis are transferred into the grain at a rate inversely proportional to **Gf**. Therefore, any increase of **Gf** will also reduce the rate of biomass remobilisation. Under stress conditions, when grain growth could be terminated as a results of leaves dying early due to water or heat stress, grain yield could decrease not only because of the reduction in intercepted radiation but also because of the

Table 1
Characteristics of 10 European sites.

Site	Country	ID	Longitude	Latitude	Annual precipitation (mm)	Minimum temperature in January	Maximum temperature in July	Cultivar	Sowing
Tylstrup	Denmark	TR	9.9	57.2	668	−2.9	19.8	Avalon	18/10
Edinburgh	UK	ED	−3.3	55.9	650	0.5	19.0	Claire	10/10
Warsaw	Poland	WS	21.1	52.1	458	−3.6	24.4	Avalon	18/10
Wageningen	Netherlands	WA	5.7	52.0	765	−0.8	21.5	Claire	01/11
Rothamsted	UK	RR	−0.35	51.8	693	0.3	20.8	Mercia	10/10
Mannheim	Germany	MA	8.6	49.5	641	−1.4	24.6	Claire	18/10
Debrecen	Hungary	DC	21.6	47.6	563	−5.5	26.3	Thesee	18/10
Clermont-Ferrand	France	CF	3.1	45.8	600	−0.7	25.5	Thesee	15/11
Montagnano	Italy	MO	11.8	43.3	752	−0.6	28.8	Creso	25/11
Seville	Spain	SL	−5.88	37.42	524	4.3	35.2	Cartaya	30/12

Table 2

Sirius cultivar parameters with the value ranges used in optimisation for high-yielding ideotypes.

Parameter	Symbol	Range	
Photosynthesis			
Light conversion efficiency	L	1–1.10 (dimensionless)	(1)
Phenology			
Phyllochron	Ph	70–140 (°C days)	(2)
Daylength response	Pp	0.05–0.70(leaf h ⁻¹) daylength)	(3)
Duration of grain filling	Gf	500–900 (°C days)	(4)
Canopy			
Maximum area of flag leaf	A	0.003–0.01 (m ² leaf m ⁻² soil)	(5)
"Stay-green"	S	1–2 (dimensionless)	
Drought tolerance			
Response of photosynthesis to water stress	Wsa	0.1–0.21 (dimensionless)	
Maximum acceleration of leaf senescence	Wss	1.2–1.9 (dimensionless)	
Root water uptake			
Rate of water uptake	Ru	1–7 (%)	(6)

(1) Using a model of canopy photosynthesis, it was shown that 10% in **L** could be achieved if λ (Rubisco specificity factor) was optimized (Zhu et al., 2010).

(2) Genetic variations of **Ph** up to 20% were observed for wheat (Ishag et al., 1998; Mossad et al., 1995).

(3) Varietal difference in number of days till heading under long and short day conditions varied between 9.74 and 107.40 in a photoperiodic response experiment (Kosner and Zurkova, 1996).

(4) Genetic variations of **Gf** up to 40% were observed for wheat (Akkaya et al., 2006; Charmet et al., 2005; Robert et al., 2001).

(5) The reported range of genetic variations for flag leaf area under unlimited water and nitrogen supplies was up to 40% (Fischer et al., 1998; Shearman et al., 2005).

(6) Large genotypic variation in root characteristics and water uptake was reported (Asseng et al., 1998; Manschadi et al., 2006).

reduction in translocation of the labile carbohydrate pool to the grain (Brooks et al., 2001; Semenov et al., 2009).

2.1.3. Canopy

Two cultivar parameters to be optimised are related to canopy, i.e. maximum area of flag leaf layer **A**, and duration of leaf senescence **S**. By varying the maximum area of the flag leaf layer, we change the rate of canopy expansion and the maximum achievable leaf area index (LAI). This in turn will change the pattern of light interception and transpiration and, therefore, will affect crop growth and final grain yield. One of the strategies to increase grain yield is to extend duration of leaf senescence and maintain green leaf area longer after anthesis, the so called "stay-green" trait (Austin, 1999; Silva et al., 2000; Triboi and Triboi-Blondel, 2002).

2.1.4. Tolerance to drought

Both daily biomass production (photosynthesis) and leaf senescence depend on the drought stress factor SF calculated daily as the ratio of actual to potential evapotranspiration. Production of new daily biomass decreases proportionally to the drought biomass reduction factor **Wsa** defined as $Wsa = SF^\beta$. By varying β , **Wsa** can change significantly, particularly, for values of SF < 0.4.

In Sirius, leaf senescence requires a cultivar-specific amount of thermal time which could be accelerated by nitrogen shortage to sustain grain filling or by water or temperature stresses. In the presence of drought stress, the rate of leaf senescence increases, because the daily increment of thermal time is modified by the drought leaf senescence factor. Earlier leaf senescence will reduce grain yield. Increasing tolerance to drought stress (reducing **Wss**) will make leaves stay green longer under water stress and potentially increase grain yield.

2.1.5. Root water uptake

In Sirius, the soil is represented by 5 cm layers and only a proportion of available soil water can be extracted from each layer by

the plant on any single day. By default, plants can extract up to 10% of available soil water from the top layer at any single day and only **Ru** (%) from the bottom layer at the maximum root depth. A faster water uptake reduces current stress experienced by the plant in anticipation of additional water coming in the form of precipitation or irrigation later in the season. In dry environments with a likely drought at the end of the growing season, a slower water uptake (lower values for **Ru**) may achieve, on average, higher yields (Manschadi et al., 2006).

2.2. Optimisation set-up

An evolutionary search algorithm was incorporated in Sirius 2010, which allows optimisation of cultivar parameters for the best performance of wheat ideotypes in a target environment. Sirius employs an evolutionary algorithm with self-adaptation (EA-SA) which is shown to be applicable for solving complex optimisation problems in a high-dimensional parameter space (Back, 1998; Beyer, 1995; Meyer-Nieberg and Beyer, 2007; Schwefel and Rudolph, 1995). EA-SA was used in the past by the authors for calibration of cultivar parameters (Stratonovitch and Semenov, 2010).

In the current study, each ideotype was represented by nine cultivar parameters described in the previous section. EA-SA optimised cultivar parameters by randomly perturbing (mutating) their values and comparing ideotypes' performance under climate change. At every step, 16 candidates (new wheat ideotypes) were generated from a 'parent' by perturbing the parent's cultivar parameters. For each of 16 new candidates, 100-year mean yield was calculated for a future climate scenario. The candidate with the highest 100-year mean yield was selected as a "parent" for the next step. A formal description of EA-SA is given in ANNEX 1. General conditions of convergence of EA-SA are given in (Semenov and Terkel, 2003). The main advantage of EA-SA, compared with genetic algorithms, is that they do not require tuning control parameters during the search, where predefined heuristic rules are unavailable or difficult to formulate in a high-dimensional space with a complex optimisation function (Back, 1998; Beyer, 1995; Semenov and Terkel, 1985).

In our study, we optimised wheat ideotypes at 10 European sites with contrasting climates, which represent wheat growing areas in Europe (Table 1). Local-scale climate scenarios, named as 2050(A1B), were based on climate projections from the HadCM3 global climate model for the A1B emission scenario for 2050 (Meehl et al., 2007). One hundred years of site-specific daily weather were generated at each site by the LARS-WG stochastic weather generator (Semenov et al., 2010). To eliminate the effect of site-specific soils from the analysis, a single soil, Hafren, with available water capacity of 177 mm was used for all locations. The sowing dates and cultivars are given in Table 1 and represent typical cultivars and sowing dates for selected sites. The objective for optimisation was to maximise the 100-year mean yield. Ideotypes with the coefficient of variation (CV) of yield exceeding 15% were excluded from the selection process. The yield increase in the past 50 years was largely a result of increase in harvest index (HI). However, there has been no systematic improvement of HI since the early 1990s. There are several estimations of theoretical maximum HI for wheat: (Austin et al., 1980) estimated this value as ~0.62 and more recent analysis (Foulkes et al., 2011) suggested using ~0.64. During optimization we discarded from selection ideotypes with the 90-percentile of HI exceeding 0.64. The stopping rule for optimisation was: (1) no further improvement was possible (the search found a local optimum, or EA-SA prematurely converged), or (2) the 95-percentile of yield (Y^{95}) exceeds 20 t ha⁻¹. All simulations were assumed to be water-limited, but no N limitation was considered.

2.3. Simulation results

2.3.1. Convergence of cultivar parameters

EA-SA is a local search algorithm which converges to one of the local maxima in a multi-dimension parameter space. To avoid convergence to a local maximum and to explore fully the parameter space, we initiated a search algorithm using multiple ‘parents’. For each of 10 sites, we used 20 parents randomly scattered in the parameter space except for one parent which has the same initial cultivar parameters as a wheat cultivar currently grown in that region. For each of 20 parents, EA-SA converged to one of the local maxima or found a wheat ideotype with the 95-percentile of yield exceeding 20 t ha^{-1} .

The optimisation function computes 100-year mean yield with additional constraints on yield CV and HI. This is a complex function which will have significantly different responses (sensitivity) to variations in cultivar parameters. It can be classified as a ‘valley’ function. EA-SA will converge quickly to an optimal value of the most sensitive cultivar parameter (or several parameters) at the bottom of the ‘valley’, leaving other parameters in a state not fully optimised. This phenomenon is known as premature convergence (Back et al., 2000). To overcome premature convergence, we adopted the following procedure. When we observed convergence of a parameter (or several parameters) to a single value for most of 20 parents, we assumed that the optimal value for this parameter was found. We assigned this optimal value to a parameter and repeated optimisation for the remaining parameters.

After one or two iterations (depending on a site) duration of grain filling **Gf**, maximum area of flag leaf **A** and the “stay-green” parameter **S** converged to near-maximum values of 900, 0.01 and 1.5, respectively. Ideotypes with a longer duration of grain filling **Gf** can potentially produce higher grain yield if green leaf area is maintained during grain filling. Ideotypes with maximum values of **A** and **S** intercept more solar radiation during the growing season because of earlier establishment of canopy at the beginning of the season and later senescence of leaves at the end of the season.

After parameters **Gf**, **A** and **S** were fixed to their optimal values, convergence was observed for two more parameters, phyllochron **Ph** and daylength response **Pp** (Fig. 1). Both of these parameters

control wheat phenology including flowering date and were responsible for shifting grain filling to the most favourable part of the season, maximising intercepted solar radiation and minimising the effect of water limitation on grain yield.

Parameters related to water-stress, i.e. maximum acceleration of leaf senescence **Wss** and response of photosynthesis to water stress **Wsa**, showed convergence only at those sites where water-limitation could have significant effect on grain yield, e.g. in SL. Root water uptake **Ru** did not converge at any of the European sites, because there is no an optimal strategy of extracting soil available water during the growing season.

Fig. 1 shows normalised values of cultivar parameters for the best ideotype at each of 10 sites optimised for the 2050(A1B) climate scenario.

2.3.2. Comparing performance

For each site, we selected the best performing ideotype out of 20 candidates and compared it with the current wheat cultivar for the 2050(A1B) climate scenario. The names of current wheat cultivars are given in Table 1. Maturity date for all optimized ideotypes was later than for current wheat cultivars by about 19 days on average with maximum of 34 days later at TR (Fig. 2A, B; for abbreviations see Table 1). The grain filling period for all ideotypes was also longer by about two weeks on average with a maximum of 3 weeks at MA. Due to a longer grain filling period, ideotypes were able to achieve higher grain yields. Fig. 2C, D shows simulated mean grain yields with the 95-percentiles for current cultivars (2C) and ideotypes (2D). Grain yields for ideotypes were 78% higher on average with a maximum of 109% yield increase at CF. Because of longer grain filling, mean harvest index (HI) across all sites for ideotypes was 0.56, which was on average 15% higher than HI simulated for current wheat cultivar (Fig. 2C, D). 95-percentiles of HI have not exceeded 0.60, which is below a theoretical maximum of 0.62–0.64 suggested in Austin et al. (1980); Foulkes et al. (2011).

By tailoring phenology to future weather patterns and improving at some sites cultivar parameters responsible for drought tolerance, i.e. **Wsa** and **Wss**, ideotypes were able to reduce the overall effects of water stress on grain yield (Fig. 3A, B). To demonstrate this, we computed a drought stress index, DSI, which is defined as a relative proportion of the yield lost due to water stress, i.e. $DSI = (Y_P - Y_{WL})/Y_P$, where Y_{WL} and Y_P are water-limited and potential grain yields. Fig. 3 presents 95-percentiles of DSI (DSI95) for the current cultivars (3A) and future ideotypes (3B). DSI95 is a yield loss due to water stress, which could be expected to occur once every 20 years on average. DSI95 was on average 52% lower for ideotypes compared with current wheat cultivars. However, soil water deficit at anthesis was on average higher for ideotypes, except for 3 sites (ED, RR and MA) (Fig. 3A, B).

3. The impact of heat and drought stress on grain set and potential grain size

The preceding analysis does not account for effects of drought and excessive heat at growth stages with particular sensitivity to stress. The most sensitive stages for grain set are associated with the processes of microsporogenesis, anther dehiscence and fertilization (as reviewed by Barnabas et al., 2008; Craufurd et al., 2013), and just after fertilization for grain size (Gooding et al., 2003). The model presented here assumes that if the crop is tolerant to drought and excessive heat around anthesis, it establishes sufficient grain numbers of adequate potential size to accommodate biomass produced during grain filling. However, the grain number can be substantially reduced if wheat is exposed to a short period of stress around meiosis, sometimes assumed to be concurrent with booting (Saini and Aspinall, 1982; Westgate et al., 1996), and during

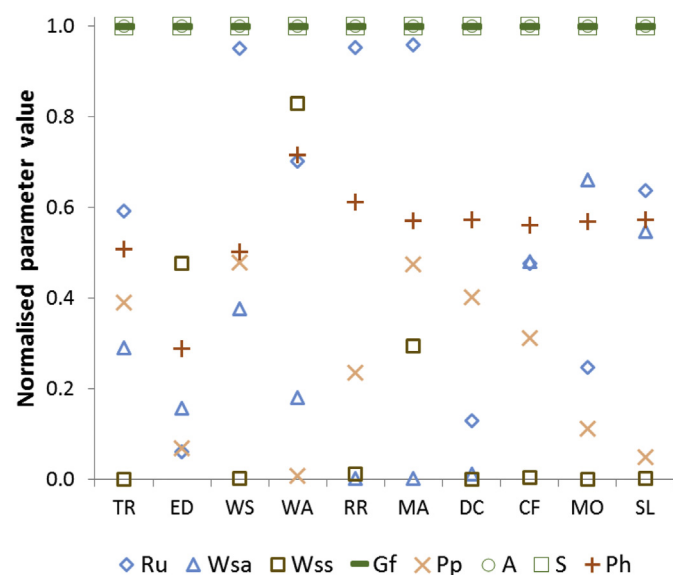


Fig. 1. Normalised cultivar parameters of the best wheat ideotypes optimised for the 2050(A1B) climate scenario at 10 European sites. Site IDs are given in Table 1, descriptions of cultivar parameters – in Table 2.

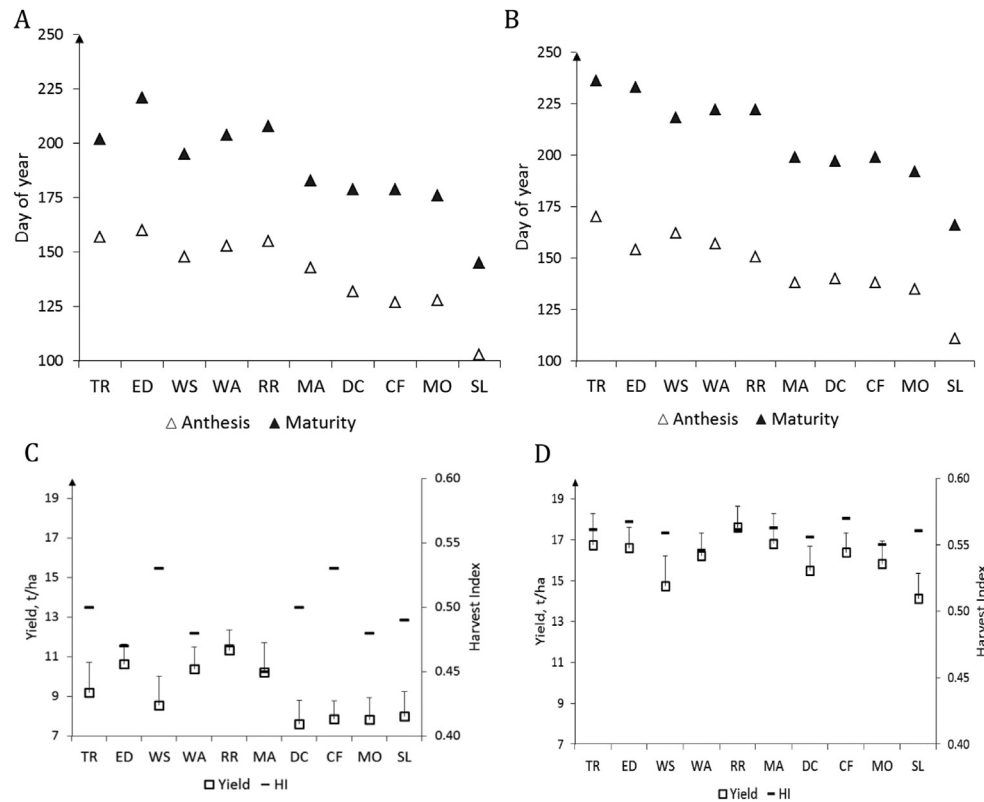


Fig. 2. (A, B) anthesis and maturity dates (day of year), and (C, D) grain yields with 95-percentiles (presented as top error bars) and harvest index (HI) as simulated by Sirius using current wheat cultivars (A, C) and future wheat ideotypes (B, D) for the HadCM3(A1B) climate scenario at 10 European locations. Information about sites is given in Table 1.

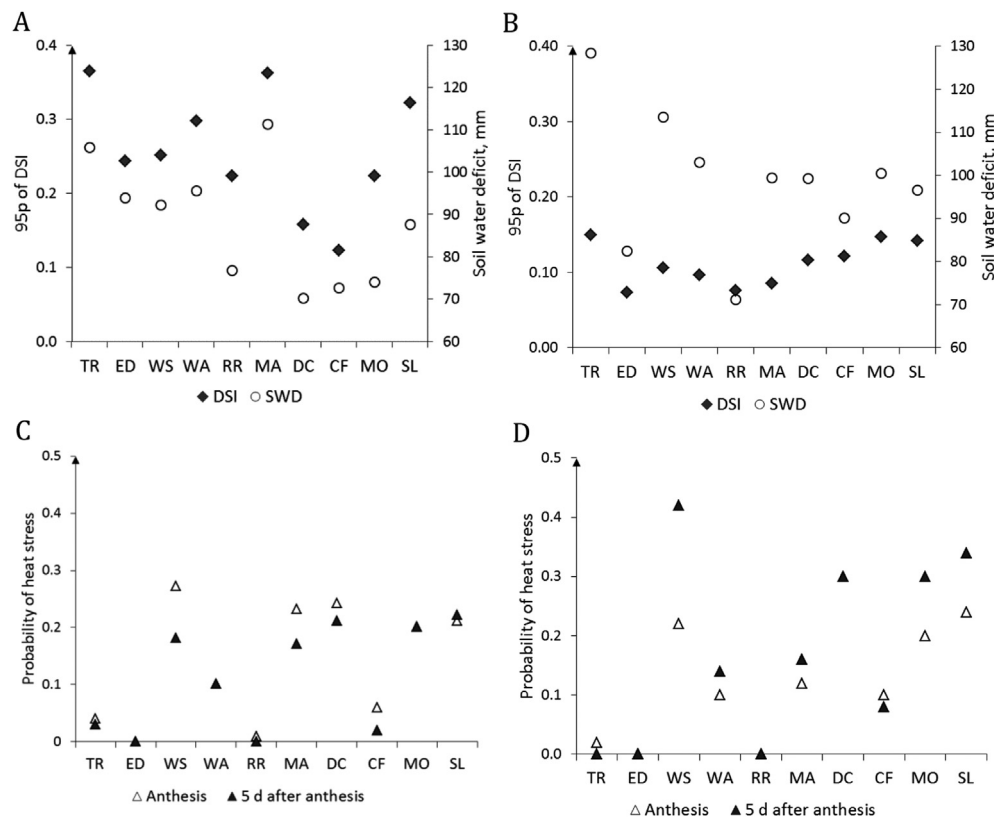


Fig. 3. (A, B) 95-percentile of drought stress index (DSI) and soil water deficit at anthesis, (C, D) probability of maximum temperature to exceed 30 °C at anthesis or 5 days after anthesis as simulated by Sirius using current wheat (A, C) cultivars and future wheat ideotypes (B, D) for the HadCM3(A1B) climate scenario at 10 European locations. Information about sites and wheat cultivars used is given in Table 1.

flowering (Wheeler et al., 1996; Ferris et al., 1998). Reductions in grain numbers or potential grain size limits the capacity of grains to store newly produced biomass. The omission of these effects contributes to an apparent inconsistency in Fig. 2, i.e. current wheat cultivars in warmer, lower latitudes flower and mature earlier (Fig. 2A), but the prediction for higher yielding ideotypes in a future warmer climate is that flowering and maturation should occur later (Fig. 2B). The earlier maturation of wheat in warmer areas is thought, in part, to be necessary to avoid heat stress events at booting and anthesis (Worland et al., 1998). More needs to be known, therefore, about the response of wheat yield to stress events at meiosis and anthesis to improve accuracy of crop models, and to identify potential for improving drought and heat stress tolerance in wheat.

Figs. 4–8 are results from three successive complete factorial replicated pot experiments (Table 3) conducted at the Plant Environment Laboratory, University of Reading, UK (51° 27' N latitude, 00° 56' W longitude), from 2010 to 2012, to compare responses of wheat for susceptibility to heat and drought stress during booting and anthesis. Further details are available (Alghabari, 2013; Alghabari et al., 2014), but in summary, factors included genotype (elite and near-isogenic lines of winter wheat varying for reduced height (*Rht*) alleles), high temperature stress (ranging from 20 °C to 40 °C), timing of stress (booting or anthesis) and irrigation (withholding water during heat stress or irrigating to field capacity (FC)). All experiments used plastic pots (180 mm diameter; 4 L volume) containing 2:1:2:0.5 of vermiculite: sand: gravel: compost mixed with Osmocote slow release granules (2 kg m⁻³) containing a ratio of 15: 11: 13:2 of N: P2O5: K2O: MgO. Weight of growing media per pot was 2.60 kg and 3.05 kg at 0 and 100% FC respectively. Plants were thinned to four plants per pot at the two leaf stage. Heat stress treatments comprised transferring pots to matched 1.37 × 1.47 m² Saxcil growth cabinets at 15:30 h GMT for three 16 h day (700 μmol photon m⁻² s⁻¹; 70 ± 2% relative humidity; 350–360 μmol CO₂ mol⁻¹ air), 8 h night cycles (8 °C below day temperature) before returning to the original, completely randomized, position outside. The approach was similar to that of Saini and Aspinall (1982) in that stress was applied for three days in an attempt to detect effects of tolerance, rather than escape due to variations in growth stage within spikes (Lukac et al., 2012). Stems in a pot were scored and tagged for their precise growth stage (GS, Zadoks et al.,

1974) when the pot was transferred. Ears tagged at different GS when transferred to the cabinets were harvested and assessed from each pot separately. Numbers of ears and spikelets were counted before the ears were threshed, cleaned and counted by hand. Fitted logistic responses ($y = c/(1 + e^{-b(t - t_5)})$) described declining grain yield and grains per spikelet with increasing t , and t_5 was that fitted to give a 5% reduction in grain set.

Stresses at booting (Fig. 4) reduced grain yield, principally by reducing grain numbers per spikelet (Fig. 4D). Partial compensation through increased mean grain weight was slight and variable (Fig. 4E) despite clement conditions and maintaining FC throughout flowering and grain filling. Critical temperatures (t_5) at booting for grains per spikelet are fitted (Fig. 4) at 32.4 °C and 24.5 °C for irrigated and non-irrigated situations respectively.

At anthesis, it appears that grain set is less susceptible to drought than at booting (Fig. 5D; Saini and Aspinall, 1981): critical temperatures fitted at 31.7 °C for the irrigated, and 29.9 °C for the non-irrigated condition. A threshold of around 30 °C is broadly consistent for the critical temperature of grain set at anthesis across a number of environments and curve fitting procedures. In an experiment on the combined effects of CO₂ and temperature on grain yield, Mitchell et al. (1993) observed that a temperature of 27 °C or higher applied mid-way through anthesis could result in a high number of sterile grains and considerable yield losses. Wheeler et al. (1996) used a temperature gradient tunnel system on field-grown wheat to demonstrate that temperatures of 30 °C or higher shortly prior to anthesis was significantly associated with reduced grain number and, subsequently, yield of cv. Hereward.

In contrast to effects at booting, drought and heat stress during flowering can reduce mean grain weight as well as grain numbers (Fig. 5E). In experiments in Australia (Tashiro and Wardlaw, 1989), plants were transferred into controlled rooms with high temperatures 7 days after the first anthers appeared, showing that a temperature of 27 °C and above could substantially reduce the maximum grain size of several Australian wheat cultivars, resulting in yield losses. It appears that the transition from a stress mainly influencing grain numbers to one which mostly affects grain size, occurs over a very narrow range of growth stages (Fig. 6). The earliest flowers on ears assessed as having just completed anthesis (GS 69) may have been fertilized four or five days earlier (Lukac, personal communication), and hence beyond the vulnerable

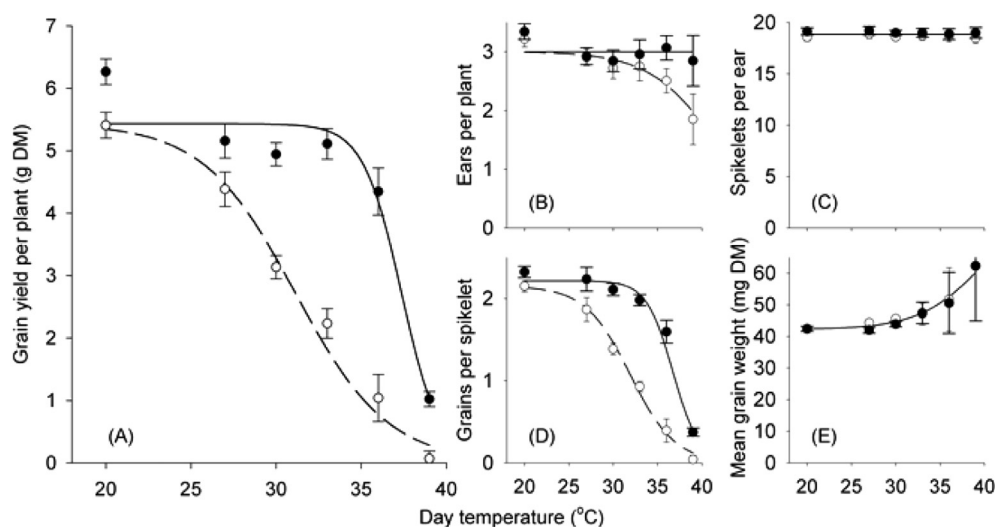


Fig. 4. Effect of day temperature and water availability (● = irrigated to field capacity; ○ = irrigation withheld) during 3 day transfers to controlled environment cabinets during booting on grain yield and yield components in winter wheat (each point is the mean of 11 genotypes, an average of 4 replicate pots and four plants per pot from Experiments 2 and 3 (Table 3)). Error bars are ±S.E.M. (70 d.f.).

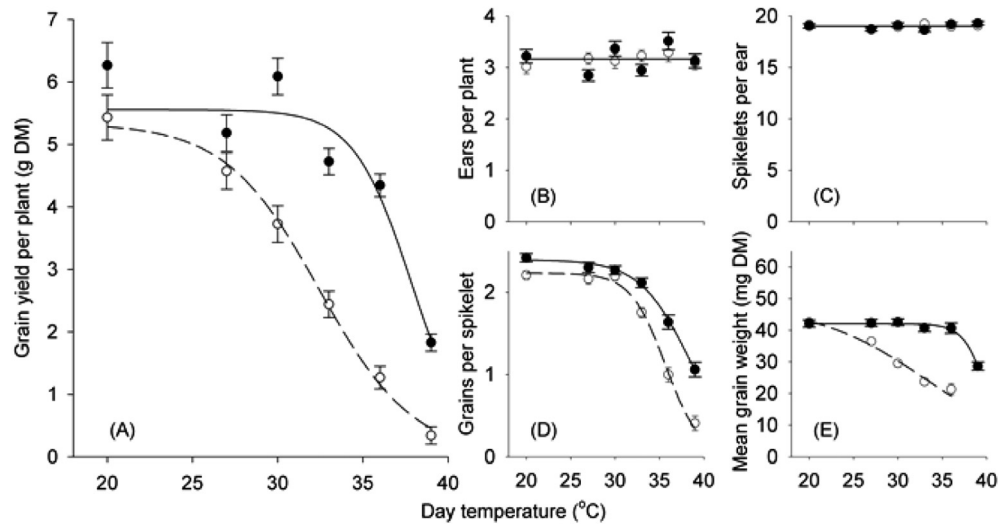


Fig. 5. Effect of day temperature and water availability (● = irrigated to field capacity; ○ = irrigation withheld) during 3 day transfers to controlled environment cabinets during booting on grain yield and yield components in winter wheat (each point is the mean of 11 genotypes, 2 replicate pots and four plants per pot from Experiment 2 (Table 3)). Error bars are ±S.E.M. (22 d.f.).

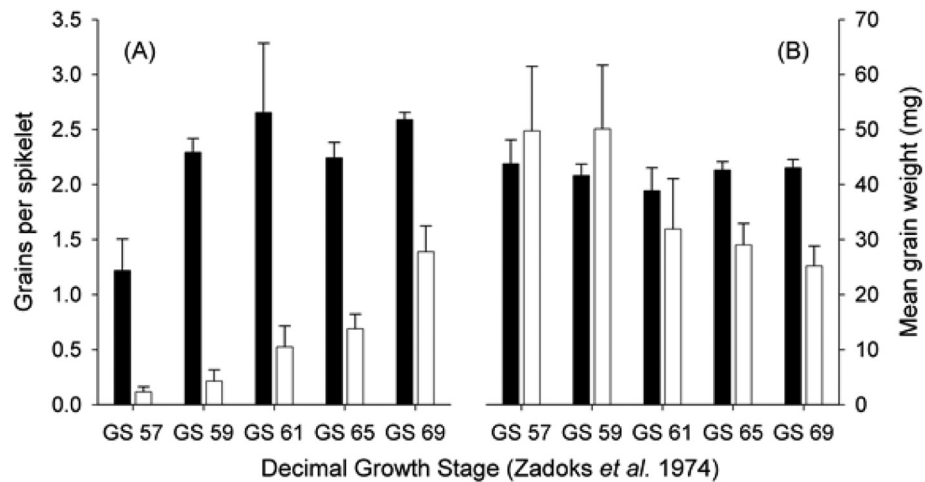


Fig. 6. Effect of ear growth stage on spikelet fertility and mean grain weight of wheat when exposed to 20 °C (solid) and 40 °C (open) with irrigation. Each bar is the mean of 11 genotypes, 2 replicate pots and four plants per pot from the anthesis treatment in Experiment 2 (Table 3). Error bars are 1 S.E.M. (22 d.f.).

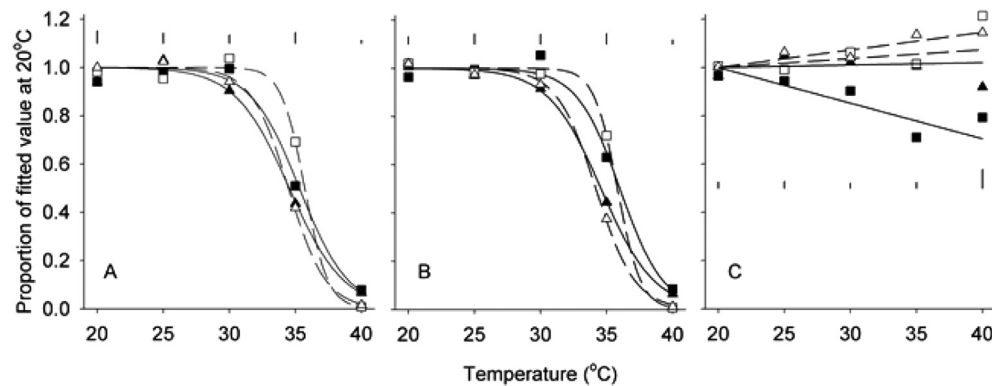


Fig. 7. Effect of day temperature during 3 day transfers to controlled environment cabinets during anthesis on (A) grain yield, (B) grains per spikelet, and (C) mean grain weight of Southern European (■ = MV Emese, ▲ = Renesansa) and UK wheats (□ = Mercia, △ = Savannah). Points are means of 6 replicate irrigated pots and four plants per pot from Experiment 1 (Table 3). Error bars are 1 S.E.M. (35 d.f.).

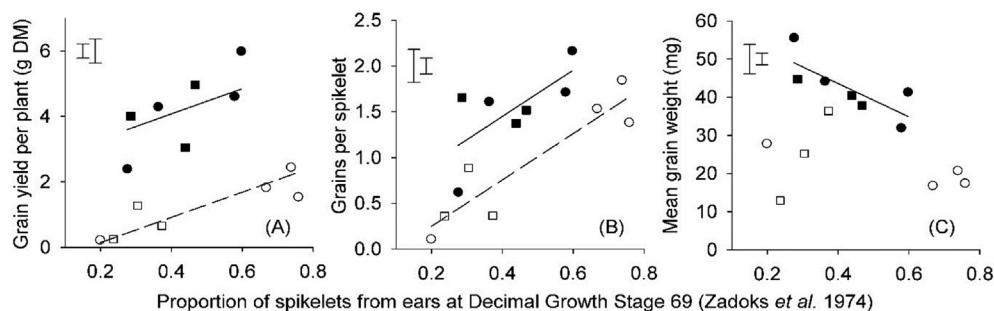


Fig. 8. Relationship between the proportion of spikelets from ears at full anthesis and performance of near-isogenic lines (NIL) of cv. Mercia varying for reduced height alleles (*Rht*) after 3-day transfers to 36°C/28 °C, 16 h day/night controlled environments with (solid) and without (open) irrigation. Squares = GA-sensitive alleles, Circles = GA-insensitive alleles. Each point is the mean for a NIL over two replicate pots, and four plants per pot from Experiment 2 (Table 3). Error bars are one SEM for without (left) and with (right) irrigation.

growth stage (Saini and Aspinall, 1982; Stone and Nicolas, 1995a,b,c) for grain set. Hence, at GS 69 it is still possible to have 1.5 grains per spikelet at temperatures as high as 40 °C under irrigated conditions. Such grains are, however, significantly reduced in final mean grain weight (Fig. 6). As well as heat there is also a large effect of drought shortly after anthesis on final mean grain weight even when subsequent water availability is high before the end of grain growth (Gooding et al., 2003).

To assess the risk of heat stress around flowering for the 2050 (A1B) climate scenario, we computed the probability of maximum temperature to exceed 30 °C at anthesis (which could affect the grain number) and the probability of maximum temperature to exceed 30 °C 5 days after anthesis (which could affect the grain size). Both probabilities are presented at Fig. 3 for the current cultivars (3C) and ideotypes (3D). Semenov and Shewry (2011) demonstrated in a modelling study that the risk of heat stress around flowering is predicted to increase in future for modern wheat cultivars in Europe and advocated to focus breeding efforts on developing heat tolerant wheat varieties to avoid a decrease in wheat yield. The risk of heat stress around anthesis was relatively high for ideotypes, between 0.1 and 0.3, (Fig. 3D) for all sites except TR, ED and RR. This means that in order to achieve the high yield potential predicted for optimized ideotypes, the heat tolerance trait needs to be incorporated in ideotypes and breeding for heat tolerance will remain a priority.

Breeding for heat and drought tolerance in wheat is non-trivial. Drought, with or without heat, can increase spike and floret concentrations of abscisic acid (ABA), which can be related closely with poor grain set (Westgate et al., 1996; Weldearegay et al., 2012).

Additionally, heat and drought can reduce photosynthesis, and the subsequent dilution of sucrose in the ear can be associated with floret abortion (as reviewed by Barnabas et al. (2008)). Furthermore, temperatures above 30 °C during meiosis can interfere with division and lead to abnormal pollen development (Saini et al., 1984). Heat shock proteins (HSPs) appear to offer some protection for mature and developing pollen grains against heat stress, when HSPs are induced by high temperatures. However, Young et al. (2001) suggest that quantities of HSPs, so induced, are often insufficient to offer full protection; and that the degree of insufficiency correlates with poor thermotolerance of pollen and reduced grain set. Pathways related to these and other processes are reviewed by Farooq et al. (2011) as potential breeding and pre-breeding targets for heat stress tolerance. What is clear is that tolerance to heat stress is greatly modified by water availability. There is a clear interaction between heat and drought (Figs. 4A and 5A). Higher temperatures increase water deficits whilst drought reduces capacity for evaporative cooling, and hence lessens possible protection from high air temperatures (Reynolds and Trethowan, 2007; Craufurd et al., 2013; Steinmeyer et al., 2013). This latter point is likely to modify the difference between DSI and SWD for future wheat ideotypes illustrated in Fig. 3B. In the field, greater water availability to the above ground crop may be achieved by selecting lines with greater investment in roots at depth compared to the surface layers (Ford et al., 2006; Wasson et al., 2012) in mature root systems. Such considerations may modify optimization of *Ru*. A further challenge for relating the results from the controlled environment work to effects likely in the field is the difficulty in simulating the responses to the more gradual

Table 3
Experimental designs for pot experiments.

Sowing date	Near isogenic (NIL) and elite lines (EL)		Treatments applied in controlled environments		Replicate pots
	Background for NILs or additional Elite line	<i>Rht</i> allele	Stress factors	Levels	
Experiment 1 24.02.10	Mercia (NIL) MV Emese (EL) Renesansa (EL) Savannah (EL)	<i>Rht</i> (tall); <i>Rht-D1b</i> ; <i>Rht-D1c</i> ; <i>Rht12</i>	Day temp. (°C) Timing Irrigation	20, 25, 30, 35, 40 Anthesis With	6
Experiment 2 24.12.10	Mercia (NIL) Maris Widgeon (NIL)	<i>Rht</i> (tall); <i>Rht-B1b</i> ; <i>Rht-B1c</i> ; <i>Rht-D1b</i> ; <i>Rht-D1c</i> ; <i>Rht8</i> ; <i>Rht12</i> <i>Rht</i> (tall); <i>Rht-B1b</i> ; <i>Rht-B1c</i> ; <i>Rht-D1b</i>	Day temp. (°C) Timing Irrigation	20, 27, 30, 33, 36, 39 Booting; anthesis With; without	2
Experiment 3 19.12.11	Mercia (NIL) Maris Widgeon (NIL)	<i>Rht</i> (tall); <i>Rht-B1b</i> ; <i>Rht-D1c</i> ; <i>Rht12</i> <i>rht</i> (tall); <i>Rht-B1b</i>	Day temp. (°C) Irrigation Timing	20, 27, 30, 33, 36, 39 With; without Booting	4

development of a drought down through the soil profile that would likely occur in the field, compared to the more dramatic ‘on/off’ availability of water imposed within the confines of a pot.

Despite the suggestions that heat stress tolerance could be improved, it is somewhat disappointing that wheats grown in Southern Europe are not necessarily more tolerant of stresses than wheats grown in the more temperate conditions of North Western Europe (Fig. 7). Currently much of the adaptation to regions that are prone to summer heat and drought is through escape, e.g. alleles such as those conferring photoperiod insensitivity, and agronomic practices such as sowing date are used to ensure booting and flowering occur before heat and drought is excessive (Worland et al., 1998; Snape et al. 2001). The plethora of genes and alleles influencing developmental rate (*Vrn-1*, vernalisation; *Ppd-1*, photoperiodism; *Eps*, earliness *per se*), their interaction, and varying sensitivities at different growth stages (Snape et al., 2001) has probably meant that adaptation through escape has been much more easy to achieve than adaptation through tolerance. Furthermore, relatively minor variations in growth stage amongst genotypes can lead to large variations in responses to stress (Fig. 8); hence apparent escape in the field may be misinterpreted as ‘tolerance’ unless detailed growth-stage scoring has been adopted. Further, wheat plants have long been known to flower throughout the day, from at least 5:00 h in the morning (Percival, 1921), so differences between genotypes in responses to stress are likely to arise through alterations in the diurnal distribution of flowering. One aspect of escape that has received little attention to date is the extent to which duration of meiosis or flowering within and/or between ears might be related to yield stability, e.g. extending the period over which a crop flowered would mean that a damaging spike in temperature would disrupt the fertilization of a smaller proportion of florets (Lukac et al., 2012). Other modelling studies have demonstrated the importance of flowering duration for estimating the impact of brief periods of high temperature on crop yield (Challinor et al., 2005) but more detailed investigation and parameter estimation would be required to assess this in a highly determinate and synchronised crop such as wheat.

4. Concluding remarks

A key factor to increase wheat yield potential is an extended duration of grain filling resulting in increased HI. This can only be possible if both capacities of the ‘sink’ and the ‘source’ are increased. The ‘source’ capacity can be increased if the plant would be able to maintain healthy green area index until the end of grain filling (‘stay-green’). In water-limited environments such as SL, improvement in drought tolerance which delays leaf senescence will be essential. The ‘sink’ capacity can be increased if the number of fertile florets at anthesis and, as a result, the number of grains at maturity increased. The floret survival rate in most wheat cultivars varies between 25% and 40%; so, in principal, there is a large potential for improvement (Gonzalez et al., 2011). Ferrante et al. (2013) studied the dynamics of floret development and its consequence on grain number and final yield in several semi-dwarf durum wheat cultivars in response to nitrogen (N) treatments and water availability. The study confirmed that increasing N availability resulted in an increased number of grains through increasing both the number of fertile florets and the percentage of them setting grains. It was shown that the fate of floret primordia in the intermediate positions of the spikelet (F3–F5) was related to the increase in assimilate supply during spike growth affected by N fertilization.

We did not consider N limitation in our simulation, assuming plentiful supply of N. However, post-anthesis N uptake and redistribution could be a serious constraint in achieving greater yield

potential. Grain demand for N during grain filling is satisfied from three sources (Jamieson and Semenov, 2000). The first is excess of N in the stem including N released by natural leaf senescence. If this amount is insufficient, then soil N is taken. Should these combined sources be insufficient, then N is remobilised from leaves reducing their photosynthetic capacity and accelerating leaf senescence (killing leaves). As a result, grain filling duration can be shortened and grain yield potential can be reduced. One of the strategies to prevent this from happening is to increase the capacity to store N in non-photosynthetic organs, such as internodes, that allows the translocation of N to grains without reducing wheat photosynthetic capacity (Bancal, 2009; Bertheloot et al., 2008; Dreccer et al., 1998; Martre et al., 2007). Another strategy would be to improve N uptake from the soil in the post-anthesis period. However, the ability of roots to take up N could decline during grain filling (Andersson et al., 2004; Martre et al., 2006; Oscarson et al., 1995). Moreover, if the end of grain filling coincides with low water availability (a typical situation in SL), then soil N available for uptake could be substantially reduced due to water shortage (Semenov et al., 2007).

A significant requirement is for a better understanding of how higher temperatures and drought stresses, particularly during the booting and flowering periods constrain sink size, either through reducing grain numbers and/or potential grain weight (Lizana and Calderini, 2013). Breeding for improved stress tolerance, particularly during meiosis and anthesis, remains a significant challenge. It would appear that much of the current adaptation of wheat to hotter and drier environments has involved ‘escape’ rather than ‘tolerance’. Some ‘escape’ strategies such as extending the duration, or modifying the diurnal pattern of susceptible stages may provide some improved stability of yield against the challenge of increased frequency of extreme events. Additionally improved water availability through, for example, more efficient root systems and architectures may provide some protection against excessive temperatures. However, maintaining or increasing resource capture and partitioning in ways predicted to be optimal by Sirius for a climate change scenario requires the development of heat tolerant varieties.

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Annex 1

A schematic representation of a variant of EA-SA used for ideotype optimization is presented in Box 1. At every discrete step of optimization, t , the evolving state, a “parent”, is described as $(\mathbf{x}, \mathbf{v}, \sigma_v, \sigma_l)$, where $\mathbf{x} \in \mathbb{C}^9$, $\mathbf{v} \in \mathbb{S}^9$, $\sigma_v \in [0,1]$, $\sigma_l \in [0,1]$, $\mathbb{C}^9 = [-1,1]^9$ and $\mathbb{S}^9 = \{\mathbf{v} \in \mathbb{C}^9, |\mathbf{v}| = 1\}$. \mathbf{x} is a vector of cultivar parameters, and \mathbf{v} is a vector controlling variation (“mutation”) for \mathbf{x} with two scaling parameters σ_v and σ_l . At each step t , a set of “offsprings” is created by mutating each parameter of a “parent” $(\mathbf{x}, \mathbf{v}, \sigma_v, \sigma_l)(t)$. The rules for mutation are specified in Box 1. Then, during selection, the “offspring” with the maximum of the “fitness” function $F(\mathbf{x}^{ij})$ is

Box 1

A schematic representation of a variant of EA-SA used for ideotype optimization.

```

EA-SA
{
  Initialise ( $\mathbf{x}, \mathbf{v}, \sigma_v, \sigma_l$ ) ( $t=0$ )
  Iterate (StoppingRule)
  {
     $\{(\mathbf{x}, \mathbf{v}, \sigma_v, \sigma_l)^{ij}(t), i < k_v, j < k_l\} = \text{CreateOffsprings}((\mathbf{x}, \mathbf{v}, \sigma_v, \sigma_l)(t))$ 
     $(\mathbf{x}, \mathbf{v}, \sigma_v, \sigma_l)(t+1) = \text{Select}\{(\mathbf{x}, \mathbf{v}, \sigma_v, \sigma_l)(t), (\mathbf{x}, \mathbf{v}, \sigma_v, \sigma_l)^{ij}(t)\}$ 
  }

  CreateOffsprings  $((\mathbf{x}, \mathbf{v}, \sigma_v, \sigma_l)(t))$ 
  {
    for ( $i < k_v$ )
    {
       $\sigma_v^i = \text{mutate}(\sigma_v)$ 
       $\mathbf{v}_i = \text{mutate}(\mathbf{v}, \sigma_v^i)$ 
      for ( $j < k_l$ )
      {
         $\sigma_l^{ij} = \text{mutate}(\sigma_l)$ 
         $\mathbf{x}^{ij} = \mathbf{x} + \sigma_l^{ij} \xi^{ij} \mathbf{v}^i$ , where  $\xi^{ij} = \text{rand}(C1)$ 
         $(\mathbf{x}, \mathbf{v}, \sigma_v, \sigma_l)^{ij}(t) = (\mathbf{x}^{ij}, \mathbf{v}^i, \sigma_v^i, \sigma_l^{ij})$ 
      }
    }
  }

  Select
  {
    if ( $F(\mathbf{x}) \geq F(\mathbf{x}^{ij})$ )
    {
       $(\mathbf{x}, \mathbf{v}, \sigma_v, \sigma_l)(t+1) = (\mathbf{x}^k, \mathbf{v}^k, \sigma_v^k, \sigma_l^{k,m})$ , where  $F(\mathbf{x}^{k,m}) = \max\{F(\mathbf{x}^{ij})\}$ 
    } else
    {
       $(\mathbf{x}, \mathbf{v}, \sigma_v, \sigma_l)(t+1) = (\mathbf{x}^{k,m}, \mathbf{v}^k, \sigma_v^k, \sigma_l^{k,m})$ , where  $F(\mathbf{x}^{k,m}) = \max\{F(\mathbf{x}^{ij})\}$ 
    }
  }

  Mutate( $\sigma$ ) { return ( $\sigma e^{\text{rand}(C1)}$ ) }

  Mutate( $\mathbf{v}, \sigma_v^i$ ) { return ( normalised( $\mathbf{v} + \sigma_v^i \text{rand}(C^n)$ ) ) }

```

selected as a parent for the next step $t+1$, $(\mathbf{x}, \mathbf{v}, \sigma_v, \sigma_l)(t+1)$. The “fitness” function $F(\mathbf{x})$ is defined as the mean yield calculated for a 100 years long climate scenario. The optimisation process stops when no further improvements of $F(\mathbf{x})$ is possible, i.e. a local optimal is found for the set of cultivar parameters. Technical details and general conditions for convergence of an EA-SA algorithm could be found in (Semenov and Terkel, 2003).

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